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Expansion or recolonization: Distribution and ecology of the pontic-mediterranean species of genus *Acrotylus* (Orthoptera) at the northern border of their range

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Abstract

Several thermophilous insect species have shown northward expansion in recent decades, and for some, it is only a matter of the recolonization of historic sites. *Acrotylus insubricus* and *A. longipes* are pontic-mediterranean species, and their northern edge is in Central Europe (Slovakia). Between 1890 and 1962, these species were known as rare in southern Slovakia, with *A. insubricus* found at five sites during that period and *A. longipes* found only once (1961) in southeastern Slovakia. Despite increased sampling efforts in Slovakia after 1997, *A. insubricus* was not documented between 1962 and 2019, and *A. longipes* was not found between 1961 and 2023. In 2016, we began regularly checking 53 sandy habitats in southern Slovakia; *A. insubricus* was found abundant in two sites in 2019 and in nine sites in 2024 and 2025, while *A. longipes* was found abundant in two sites in 2023 (Aug 21-Nov 3) and in three in 2024 and 2025 (Jun 21–Oct 25), always accompanied by *A. insubricus*. Recently, the edge of the northernmost range of *A. insubricus* in Central Europe was 48.53°N, and for *A. longipes*, it was 48.40°N. In this paper, we describe the distribution, abundance, phenology, and habitat of both species. Regarding habitat, *A. longipes* needs sandy bare ground with sparse psammophilous vegetation and impacted frequently by human interference, while *A. insubricus* is more eurytopic and also occurs on rocky steppes. We found only *A. insubricus* adults overwintering in all nine sites, but never *A. longipes*, which is different behavior than that of these species in the southern parts of the range. We suggest that *A. insubricus* and *A. longipes* have recolonized historical sites and spread into sandy, human-disturbed habitats.

Keywords

abundance, Acrididae, biogeography, distribution, ecology, wintering

Introduction

In recent decades, knowledge about the spreading or recolonization of thermophilic insect species in Europe, as well as the factors that might have triggered them, has been increasing (Löffler et al. 2019, Kaláb et al. 2021, Hällfors et al. 2024). Furthermore, increasing relative abundance and expansion of the area where thermophilous Orthoptera species (e.g., *Acrida ungarica*, *Calliptamus italicus*, *Euchorthippus declivus*, *Omocestus petraeus*, and *Platycleis affinis*) are found has also been detected (Kenyeres et al. 2019, 2023).

The thermophilic and xerophilous species of the genus *Acrotylus* have a typical African and pontic-mediterranean distribution, yet the northern limits of their distribution ranges remain poorly known (Rácz 1998, Hochkirch et al. 2016, Bellmann et al. 2019, Balla and Krištín 2019). The origin of the population in the north of the range in Central Europe has been debated for a long time (Nagy 1958, 1974). The Common Digging Grasshopper *Acrotylus insubricus* (Scopoli, 1786) is widely distributed in Africa and Eurasia, but in Europe, it is found only in its southern regions, mainly in the Mediterranean (Harz 1975, Hochkirch et al. 2016, Willemse et al. 2018, Bellmann et al. 2019, Fig. 1). The northern border of the range is marked by some isolated localities in southern Slovakia (Mařan 1954, Čejchan 1961, Hochkirch et al. 2016, Balla and Krištín 2019), while it has been found in Hungary in many localities (Rácz 1986, Nagy 2005, Dobos 2025, https://www.inaturalist.org/). The Yellow-winged Digging Grasshopper *Acrotylus longipes* has a more fragmented distribution than *A. insubricus*, occurring mainly in the Eastern Mediterranean as well as in North Africa and Western Asia. In Europe, it is found in southern Italy and the Balkans. Isolated distribution is also known from the Canary Islands (Harz 1975, Hochkirch et al. 2016, Willemse et al. 2018, Bellmann et al. 2019, Fig. 1). At the northern limit of the range, it has a severely fragmented distribution, limited to blown and alluvial sands. For instance, in Hungary, it is found in two areas (Nagy 1958, 1959, Rácz 1986, Dobos 2025, https://www.inaturalist.org/), while in NE Hungary, it has recently been reported as extinct (Hochkirch et al. 2016, www.iNaturalist.com). In Croatia, only three sites are known—all along the Adriatic Sea (Papković and Jelinčić 2019)—and in Slovakia, the only published occurrence was recorded in 1961 (Gulička 1992, Gulička, in litt). The distribution of both species in Ukraine was unknown until Harz (1975) reported their occurrence in the SW part of the country.

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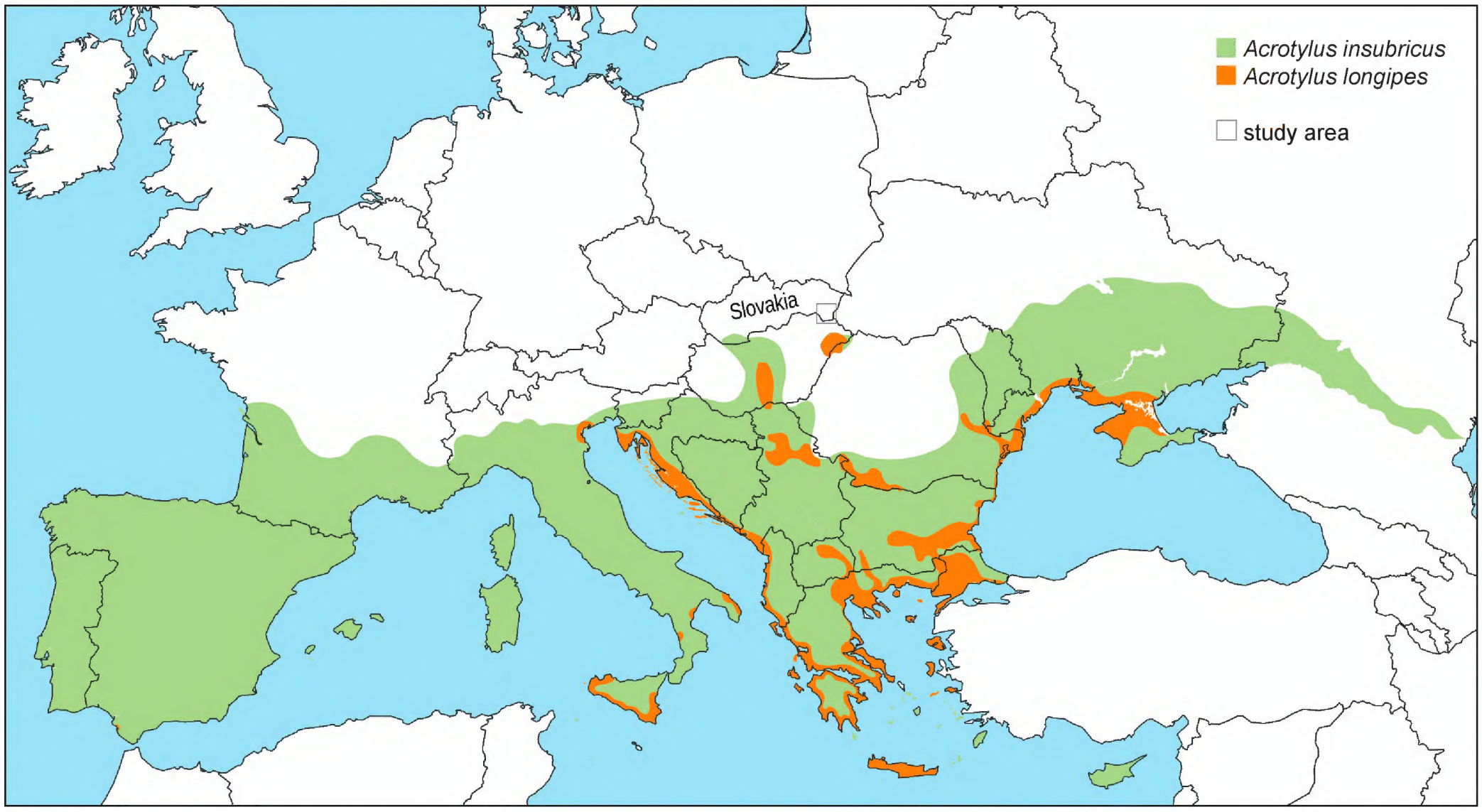


Fig. 1. Range of *A. insubricus* (green) and *A. longipes* (orange) in continental Europe (following Hochkirch et al. 2016) and study area in southeastern Slovakia (square).

It remains unclear whether *A. insubricus* and *A. longipes* are currently spreading or recolonizing historically known areas on the northern border of their distribution range. Thus, *A. insubricus* was detected on the northern border of the range only after 57 years (in 2019) in SE Slovakia, despite regular field research since 1997 in Orthoptera-suitable habitats in 53 localities in southern Slovakia (Balla and Krištín 2019). In addition, in 2023–2025, we recorded (after 62 years) *A. longipes* in three localities in SE Slovakia. Data on the abundance, ecology, phenology, and wintering strategy of both species at the northern edge of the distribution range are also very scarce (Mařan 1954, Nagy 1958, 1974, Čejchan 1961, Hochkirch et al. 2016, Krištín et al. 2020, https://www.inaturalist.org/). Here, the breeding distribution of *A. longipes* is confined to the blown and alluvial sands, while *A. insubricus* also occurs in xerothermic rocky steppes and forest-steppe habitats (Čejchan 1961, Nagy 1958, 1959, Hochkirch et al. 2016).

Therefore, in addition to a long-term distribution study, we focused on the abundance, phenology, and ecology of both species in Slovakia in 2023 and 2024 and in spring 2025. We studied the occurrence of species at 53 potential localities in southern Slovakia. The abundance and phenology were studied mainly at two selected sites of blown sands in southeastern Slovakia, and the habitats and accompanying Orthoptera and Mantodea assemblages were studied at all nine sites of *A. insubricus* occurrence, three of which were shared by *A. longipes*.

Materials and methods

Due to the historical occurrence of the two studied species, all orthopterological literature from the second half of 19th century was reviewed (from Frivaldszky 1867 and Chyzer 1897). Research on the recent distribution of species was carried out within the framework of the mapping of Orthoptera of Slovakia (www.orthoptera.sk, Krištín 2025), when data were obtained from ca. 4500 sites in Slovakia between 1994 and 2024. From March to November in 1997–2024, we irregularly mapped Orthoptera in 53 localities of southern Slovakia at historical and potential localities of both species (5–28 localities per year, Krištín et al. 2004a, b, 2011, Krištín and Balla 2021). We discovered *A. insubricus* in 2019 after 22 years of mapping (Balla and Krištín 2019) and *A. longipes* in 2023 after 26 years. The published data on both species from Slovakia are missing for 1962–1994 due to irregular and insufficient mapping of the Orthoptera of Slovakia during that time period.

After discovery of the first breeding population of *A. insubricus*, we monitored the occurrence and abundance of species of the genus *Acrotylus* and other Orthoptera at 16 potential sites in SE Slovakia from 2019 to 2024 at 1–2 monthly intervals (February–November). During this time, we mapped (1–2 times a year) 12 locations in southwestern and central Slovakia, where the occurrence of the genus *Acrotylus* had been recorded in the past or has been expected in connection with the occurrence of other psammophilous species (Mařan 1954,1958, Čejchan 1961, Gulička 1992, Krištín et al. 2004a, b, Kenyeres et al. 2023). Orthoptera and Mantodea were sampled primarily by sweeping the herbaceous layer and, partially, the shrub vegetation. This was supplemented with individual collection and acoustical identification of specimens. All the sites (up to 50 m from the nearest occurrence of *Acrotylus* individuals) were checked in a checkerboard pattern (about 60 min per check) by 1–3 experts. The maximum observed abundance per check of all the Orthoptera and Mantodea species was evaluated in seven semiquantitative abundance categories over six years (2019–2024) at all nine known *A. insubricus* sites, including three sites of co-occurrence with *A. longipes* (Table 1).

Table 1. Orthoptera assemblages at nine *A. insubricus* and *A. longipes* Slovak sites in 2019–2024 (F% = frequency of occurrence at 9 sites; maximum abundance per check in species is given in relative semiquantitative categories as: 1: 1 ind., 2: 2 ind., 3: 3–10 ind., 4: 11–25 ind., 5: 26–50 ind., 6: 51–100 ind., 7: > 100 ind.; habitat: SQ: sand quarry, SD: blown sand, XS: xeric rocky steppe, LQ: limestone quarry; disturbance type of habitat: D – disturbed, SN – seminatural, N – natural.*

Site No.	1	2	3	4	5	6	7	8	9	
Site name	Biel	Somotor	Svätuše	Horeš	Kapoňa	Beša	Vojka	Kamenec	Ladmovce	%F
Habitat	SQ	SD	SD	SD	SD	SD	SD	XS	LQ	
Disturbance type	D	N	SN	N	SN	SN	SN	SN	D	
Conocephalus dorsalis (Latreille, 1804)	–	3	–	–	–	2	–	–	–	22
Conocephalus fuscus (Fabricius, 1793)	3	3	1	3	3	1	2	2	–	89
Decticus verrucivorus (Linnaeus, 1785)	–	–	3	3	2	1	3	4	2	78
Ephippiger ephippiger (Serville, 1831)	–	–	–	–	–	–	–	2	2	22
Gampsocleis glabra (Herbst, 1786)	–	3	4	3	–	3	–	–	–	44
Isophya kraussii Brunner von Wattenwyl, 1878	–	–	–	–	–	–	–	2	–	11
Leptophyes albovittata (Kollar, 1833)	5	4	4	5	4	4	5	6	4	100
Leptophyes discoidalis (Frivaldszky, 1867)	–	–	–	–	–	–	–	–	2	11
Meconema thalassinum (Degeer, 1773)	–	–	–	–	–	2	–	2	2	33
Bicolorana bicolor (Philippi, 1830)	–	–	–	3	3	2	1	4	3	67
Roeseliana roeselii (Hagenbach, 1822)	2	2	2	4	3	3	3	4	2	100
Phaneroptera falcata (Poda, 1761)	–	–	–	2	–	–	–	2	1	33
Phaneroptera nana Fieber, 1853	–	1	2	2	2	2	2	2	–	78
Pholidoptera griseoaptera (Degeer, 1773)	–	–	–	2	–	–	–	3	2	33
Platycleis affinis Fieber, 1853	–	4	3	3	–	2	3	–	–	56
Platycleis grisea (Fabricius, 1781)	4	4	3	4	4	3	2	5	5	100
Montana montana (Kollar, 1833)	–	–	2	2	–	1	–	3	–	44
Tesselana veyseli (Koçak, 1984)	–	–	2	2	–	–	–	–	–	22
Poecilimon schmidti (Fieber, 1853)	–	–	–	–	–	–	–	1	–	11
Ruspolia nitidula (Scopoli, 1786)	3	3	2	3	2	3	2	3	–	89
Tettigonia caudata (Charpentier, 1842)	–	3	4	3	–	–	–	–	–	33
Tettigonia viridissima Linnaeus, 1758	2	3	2	2	3	2	3	3	–2	100
Gryllotalpa gryllotalpa (Linnaeus, 1758)	1	1	–	–	2	2	1	–	–	56
Eumodicogryllus bordigalensis (Latreille, 1804)	–	1	1	1	1	–	–	1	–	56
Gryllus campestris Linnaeus, 1758	2	3	5	4	5	4	4	5	3	100
Melanogryllus desertus (Pallas, 1771)	2	3	3	3	2	–	–	–	2	67
Modicogryllus frontalis (Fieber, 1844)	–	–	–	–	–	–	–	1	–	11
Oecanthus pellucens (Scopoli, 1763)	3	4	5	5	4	4	4	5	4	100
Pteronemobius heydenii (Fischer, 1853)	2	–	–	–	–	2	–	–	–	22
Xya pfaendleri (Harz, 1970)	4	–	–	–	–	3	–	–	–	22
Xya variegata Latreille, 1809	4	–	–	–	–	–	–	–	–	11
Tetrix bipunctata (Linnaeus, 1758)	–	–	–	1	–	–	–	–	–	11
Tetrix bolivari Saulcy, 1901	3	1	–	–	–	3	2	–	–	44
Tetrix subulata (Linnaeus, 1758)	–	–	–	–	–	1	–	1	–	22
Tetrix tenuicornis (Schalberg, 1893)	3	2	2	2	–	–	3	2	–	67
Acrida ungarica (Herbst, 1786)	–	6	4	4	–	–	–	–	1	44
Acrotylus insubricus (Scopoli, 1786)	7	7	6	3	6	3	6	3	3	100
Acrotylus longipes (Charpentier, 1845)	7	7	3	–	–	–	–	–	–	33
Aiolopus thalassinus (Fabricius, 1781)	–	5	2	3	2	3	–	–	–	56
Calliptamus italicus (Linnaeus, 1758)	7	7	7	6	6	6	6	7	7	100
Chorthippus apricarius (Linnaeus, 1758)	–	2	–	3	3	–	–	1	–	33
Chorthippus biguttulus (Linnaeus, 1758)	3	3	3	4	3	3	2	4	5	100
Chorthippus brunneus (Thunberg, 1815)	4	4	4	4	4	4	3	5	4	100
Chorthippus dichrous (Eversman, 1859)	–	6	–	3	–	2	–	–	–	33
Chorthippus dorsatus (Zetterstedt, 1821)	3	3	3	3	4	3	3	2	–	89
Chorthippus mollis (Charpentier, 1825)	2	4	3	3	4	4	4	5	4	100
Chorthippus oschei Helversen, 1986	2	3	2	3	3	3	3	–	–	78
Pseudochorthippus parallelus (Zetterstedt, 1821)	–	3	–	3	3	3	1	3	–	67
Chrysochraon dispar (Germar, 1834)	–	2	–	–	–	2	1	2	–	44
Dociostaurus brevicollis (Eversmann, 1848)	4	5	6	5	5	6	5	4	–	89
Euchorthippus declivus (Brisout de Barneville, 1848)	–	–	4	6	4	3	2	5	4	78
Euchorthippus pulvinatus (Fischer von Waldheim, 1846)	–	2	2	3	1	1	–	2	–	67

Site No.	1	2	3	4	5	6	7	8	9	
Site name	**Biel**	**Somotor**	**Svätuše**	**Horeš**	**Kapoňa**	**Beša**	**Vojka**	**Kamenec**	**Ladmovce**	**%F**
Habitat	**SQ**	**SD**	**SD**	**SD**	**SD**	**SD**	**SD**	**XS**	**LQ**	
Disturbance type	**D**	**N**	**SN**	**N**	**SN**	**SN**	**SN**	**SN**	**D**	
Euthystira brachyptera (Ocskay, 1826)	–	–	–	–	1	–	–	3	–	22
Gomphocerippus rufus (Linnaeus, 1758)	–	–	–	–	–	–	–	3	–	11
Mecostethus parapleurus (Hagenbach, 1822)	2	4	2	5	–	4	3	–	–	67
Myrmeleotettix antennatus (Fieber, 1853)	–	1	–	2	–	2	–	–	–	33
Myrmeleotettix maculatus (Thunberg, 1815)	–	4	4	5	–	5	4	–	–	56
Oedaleus decorus (Germar, 1826)	1	3	5	4	–	2	3	–	–	67
Oedipoda caerulescens (Linnaeus, 1758)	4	6	5	6	4	5	4	5	5	100
Omocestus haemorrhoidalis (Charpentier, 1825)	–	2	2	3	–	1	–	3	4	67
Omocestus petraeus (Brisout de Barneville, 1856)	–	1	1	2	–	–	–	2	–	44.4
Omocestus rufipes (Zetterstedt, 1821)	–	2	4	4	–	2	2	1	–	66.7
Sphingonotus caerulans (Linnaeus, 1767)	–	–	–	–	–	–	–	–	4	11
Stenobothrus crassipes (Charpentier, 1825)	2	4	4	4	2	4	1	3	4	100
Stenobothrus lineatus (Panzer, 1796)	–	–	–	3	–	–	–	2	2	33
Stenobothrus nigromaculatus (Herrich-Schäffer, 1840)	–	2	3	5	–	2	–	3	4	67
Stethophyma grossum (Linnaeus, 1758)	–	2	–	2	–	3	–	–	–	33
Mantis religiosa (Linnaeus, 1758)	3	4	4	4	2	4	2	4	2	100
Number of Species	29	46	41	50	31	46	33	44	28	–

*The geographical coordinates of sites are not listed for conservation reasons and the occurrence of several extremely rare species.

The study sites with the occurrence of the genus *Acrotylus* (N = 9) were divided into three categories according to the degree of disturbance (considering the vegetation type and type of management) with the degree of occurrence prevailing on the site (> 90% of the site): Mostly protected sites (NATUR) were those with native plant cover and with nearly no signs of destructive management during the last 30 years. Semi-natural sites (SEMINATUR) were mostly extensive pastures with preserved psammophilous vegetation, and disturbed sites (DISTURB) were those with signs of intensive changes in substrate and vegetation cover. The sites are characterized as follows: (1) Preserved sand dunes with characteristic sparse, low-grown sandy herb- and grass-dominated vegetation with scattered scrub and few depressions filled with wetland vegetation (two NATUR sites: Somotor, Malý Hore), (2) Extensively grazed and partially ruderalized sand dunes with characteristic sparse low-grown herbaceous vegetation (four SEMINATUR sites: Svätuše, Kapoňa, Beša, Vojka), (3) Abandoned formerly mined sand pits on sand dunes with depressions and aquatic vegetation (DISTURB site Biel), (4) Abandoned limestone quarry (DISTURB site Ladmovce), and (5) Preserved rocky steppic grasslands and forest-steppe woodlands on andesite rock (SEMINATUR site Malý Kamenec; Table 1).

In addition, we studied the phenology and overwintering (as winter and early spring occurrence of adults) of both species three times per month at two sites (Biel and Somotor) in February–November 2023 and 2024 and February–April 2025.

Results and Discussion

Distribution in Slovakia.—The first records of *A. insubricus* in Slovakia, at the northern limit of the species' range, date back to the end of the 19th century, when data from Somotor (SE Slovakia) were published (Chyzer 1897). From 1951–1961, new data were collected from the same two sites and from three other sites in SW Slovakia (Mařan 1954, Čejchan 1961, Gulička 1992; Fig. 2A). Orthoptera mapping data from Slovakia from 1962–1994 are missing. The first finding of the species since we began regular data collection in 1997 was in 2019, when it was detected in two sites in SE Slovakia (Balla and Krištín 2019); subsequently, it was found in 7 sites in 2020–2022 and in 9 sites out of 16 in 2023–2025 in southeastern Slovakia. None were found in the 12 historical or potential sites in southwestern and central Slovakia (Fig. 2). However, there was species occurrence in northern Hungary (Göd) 35 km southeastern of the nearest historical southwestern Slovak site, and in eastern Hungary (Debrecen E) 100 km south of the southeastern Slovak populations (Fig. 2A). These could be seen as potential source populations for the species' recolonization in Slovakia (Balla and Krištín 2019, www.inaturalist.org). The convex polygon of the most distant sites in Slovakia occupied by *A. insubricus* currently covers 206 km^2.

The history of the occurrence of *A. longipes* in Slovakia dates back to 1961, when the species was first recorded in what was then Czechoslovakia from the southeastern Slovak site (nearby Kráľovský Chlmec) without sampling details (Gulička 1992, probably August 1961, Gulička, in litt.). In 2023, we found abundant populations of the species at two sites (about 16.5 km apart) in the same area as part of a mapping campaign that began in 1997. In 2024, a third population occurrence record was added (9 km and 7 km apart from the previous two sites) from the 16 monitored localities of southeastern Slovakia. However, we have not found *A. longipes* at any of the 8 potential sandy localities of southwestern and central Slovakia thus far (Fig. 2B). The convex polygon of the most distant sites in Slovakia occupied by *A. longipes* covers 26 km^2.

There have also been two recent isolated findings of individuals relatively far from the distribution area and known localities in southeastern Slovakia and in atypical habitats. One was in 2021 (1 female, Aug 3, 2021, Jósvafö N, Aggtelek karst HU, forest steppe, 30 m from the Slovak border, 100 km west of the nearest Slovak site, Szövényi G., in litt.) and the other was in 2023 (1 female, Aug 8, 2023, Stakčín, building in the city, Slovakia, 80 km north of the nearest Slovak site, Štofík J. and Jarčuška B. in litt.). These two isolated and accidental occurrences of individuals demonstrate the species' high mobility, but subsequent checks did not provide evidence of colonization at the given localities. In Hungary, two isolated and accidental occurrences were recorded in atypical habitats in the center of Budapest and Kerepes (Fig. 2B), while other recent observations south of Budapest confirm this species distribution, as shown in Fig. 1 (Hochkirch et al. 2016).

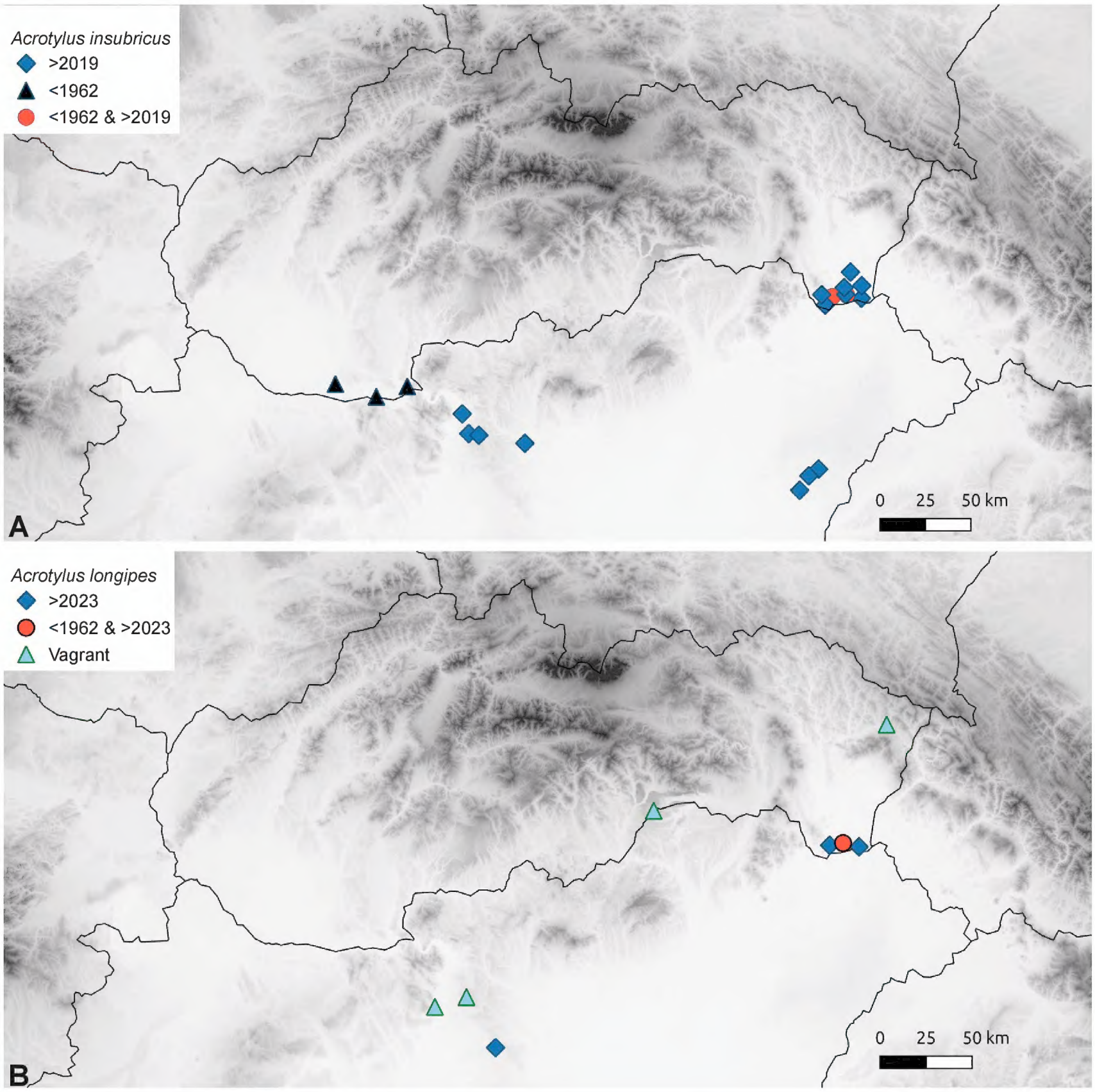
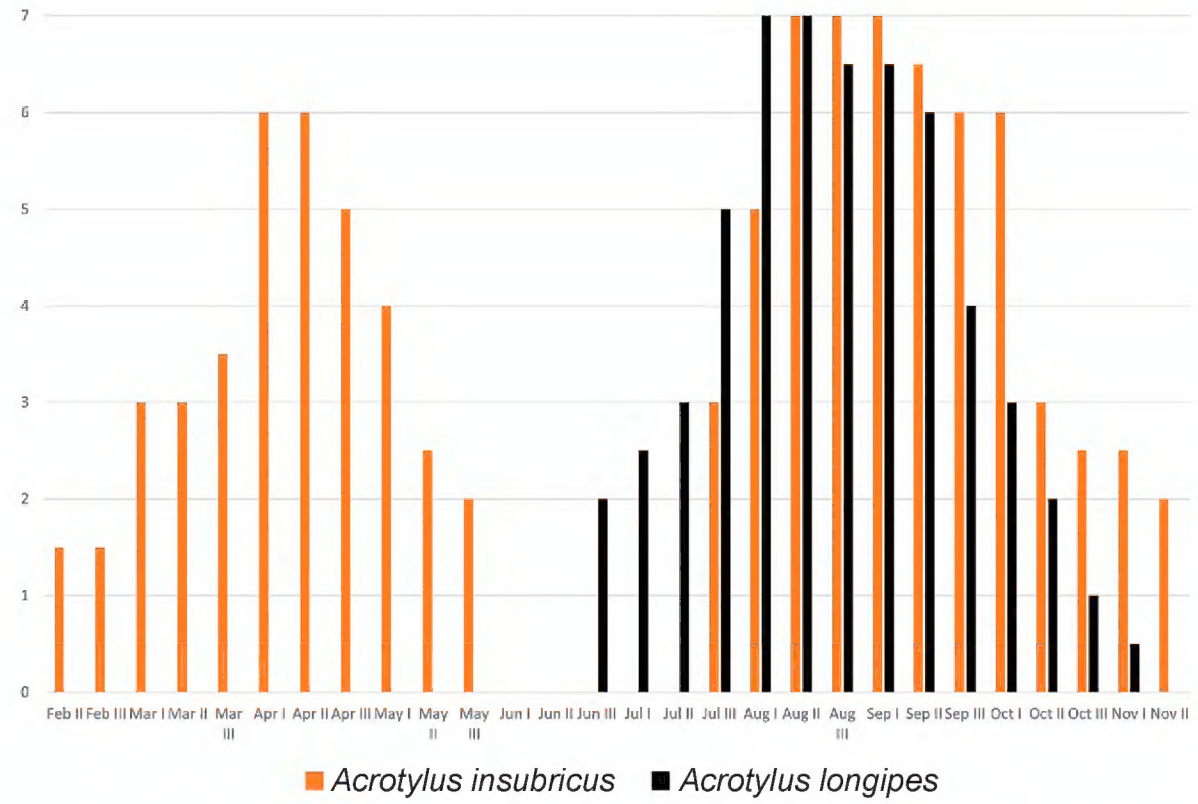


Fig. 2. Breeding distribution of *A. insubricus* (**A**) and *A. longipes* (**B**) in Slovakia and northern Hungary up to 47.3°N (black triangle: historical data before 1962, blue diamond: data from 2019–2025 for *A. insubricus*, data from 2023–2025 for *A. longipes*, red circle: data from both periods) and accidental findings of one specimen *A. longipes* outside the breeding area in 2021 and 2023 (light blue triangle). For data from Hungary, see www.iNaturalist.org.

Thus, the northernmost edge of the breeding range of *A. insubricus* in Central Europe is found at 48.53°N, (spanning elevations 98–185 m a.s.l.), and the northernmost edge for *A. longipes* is 48.40°N (spanning 98–125 m.a.s.l.). This means that the northern boundaries of both species' ranges have not changed (for *A. insubricus* since 1897 and for *A. longipes* since 1961). It also appears that both species have recolonized only their previously known territory (Fig. 2A, B). However, in *A. insubricus*, the recent northernmost breeding site (Beša) is 13 km north of the historical sites (from 1890 and 1960). We expect that the Slovak breeding sites of both species are in contact with blown sand sites in northeastern Hungary, but inspections in 2023–2024 of sites suitable for these species in this area revealed no populations.

Abundance, phenology, and wintering strategy.—Both species were mostly abundant at the sites from 2023–2025. *A. insubricus* reached a maximum abundance of > 100 adults per hectare in August and September at two of the nine sites, 50–100 adults/ha at three other sites, and < 10 adults per hectare at the remaining four sites (Table 1). Locally (the Biel and Somotor sites), the species reached densities of 20–30 specimens per 100 m^2 in August–September and generally showed lower abundance at all the sites in spring (the highest values were recorded on April 9–11, 2024). *A. longipes* reached a maximum abundance of > 100 adults per hectare (locally, 10–20 ad./100 m^2) in two out of the three breeding sites in southeastern Slovakia, mainly in August and early September (Fig. 3).

Data on the phenology and overwintering of adults of both species vary considerably in the literature. Bellmann et al. (2019) described both species as generally overwintering as adults, while Harz (1975) suggested that they do so only in the southern reaches of the distribution range. Nagy (1958) examined populations in Hungarian localities and found that even under laboratory conditions, only adults of *A. insubricus* overwinter; this has never been found in *A. longipes*, but there is no current information on their overwintering in Hungary. We confirmed the overwintering of only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Acrotylus insubricus
Acrotylus longipes

Fig. 3. Seasonal distribution and abundance of two *Acrotylus* species (adults only) at the northern range border from February 2023 to April 2025 (mean semiquantitative abundance per site from two sites (Biel and Somotor) in southeastern Slovakia. Abundance 1: 1 ind., 2: 2 ind. 3: 3–10, 4: 11–25, 5: 26–50, 6: 51–100, 7: > 100 ind./ha).

A. insubricus adults in our Slovak localities in the northern reaches of the distribution range, corroborating Nagy (1958) (Fig. 3). Identifiable nymphs of *A. insubricus* were found only from July to September. In *A. longipes*, identifiable nymphs were found in Slovakia from the beginning of June and adults from the end of June (Fig. 3).

Based on the shorter seasonal occurrence, *A. longipes* appears to have a narrower climatic niche in the northern reaches of the distribution range, with a lower number of adult individuals from June 21 to November 3 than *A. insubricus*. *A. insubricus* not only overwinters in the adult stage and then occurs from February 16 to May 21 but was also found in the same sites in autumn for a longer period (until November 20) and in greater numbers than *A. longipes* (Fig. 3).

Habitats and accompanying Orthoptera and Mantodea assemblages in southeastern Slovakia.—In the northern reaches of its distribution range in Slovakia, *A. longipes* seems to be strongly stenotopic, and breeding populations have recently inhabited only three sites and habitats of blown sands with fine material and scattered low-grown herbaceous vegetation. One of these sites is natural, the other seminatural, and the third site is situated in an abandoned sand quarry. In the past, the species was known from only one natural locality (Fig. 4). *A. insubricus* is abundant in the same habitats but rarely occurs in other xeric rocky steppes (one site on limestone and one on andesite) and in forest–steppe localities (two from nine localities). Hence, two of the nine localities have a natural character, five are seminatural, and two have been significantly disturbed by human interference over the past 60 years (Fig. 4). Thus, we can conclude that both species are able to colonize seminatural and disturbed habitats. Three sites of common breeding populations of both species are blown sands with varying degrees of human interference, spanning extensively exploited to abandoned sand quarries and preserved sand dunes exposed to extensive sheep grazing (Fig. 5A, B).

At nine sites of *A. insubricus* occurrence (three of which include *A. longipes*), we found 67 species of Orthoptera (29 Ensifera and 38 Caelifera, constituting ca. 51% of the orthopteran fauna of Slovakia) and one mantid (*Mantis religiosa*) (Table 1). In total, 28–50 species per site were recorded (an average of 39 ± 8 species), which is an exceptionally high number of species per site in Central Europe (Krištín et al. 2020). Grasshoppers (Caelifera) predominate in terms of species richness and abundance due to the steppic character of most localities. Characteristic species also include other psammo- and pseudo-psammophilous species, such as *Gampsocleis glabra, Platycleis affinis, Acrida ungarica, Dociostaurus brevicollis, Myrmeleotettix antennatus,* and *Oedaleus decorus.* Rare species of European Orthoptera were also found, including *Leptophyes discoidalis, Montana montana, Tesselana veyseli, Tettigonia caudata, Omocestus petraeus,* and *Chorthippus dichrous*.

Euryecous species, such as the bush-crickets *Leptophyes albovittata, Roeseliana roeselii, and Platycleis grisea;* crickets *Gryllus campestris* and *Oecanthus pellucens,* and grasshoppers *Calliptamus italicus, Stenobothrus crassipes, Chorthippus brunneus, Ch. biguttulus,* and *Ch. mollis,* were the most frequent at the nine study sites.

Rare European psammophilous Orthoptera have previously been found in the northern localities of the genus *Acrotylus* (cf. Chyzer 1897, Mařan 1954, Gulička 1992) (Table 1). However, this study did not confirm the historical occurrence of *Celes variabilis* (Chyzer 1897) or *Calliptamus barbarus* (Mařan 1954, 1958), which are currently absent from the northern borders of the historical range of *Acrotylus* (Hochkirch et al. 2016).

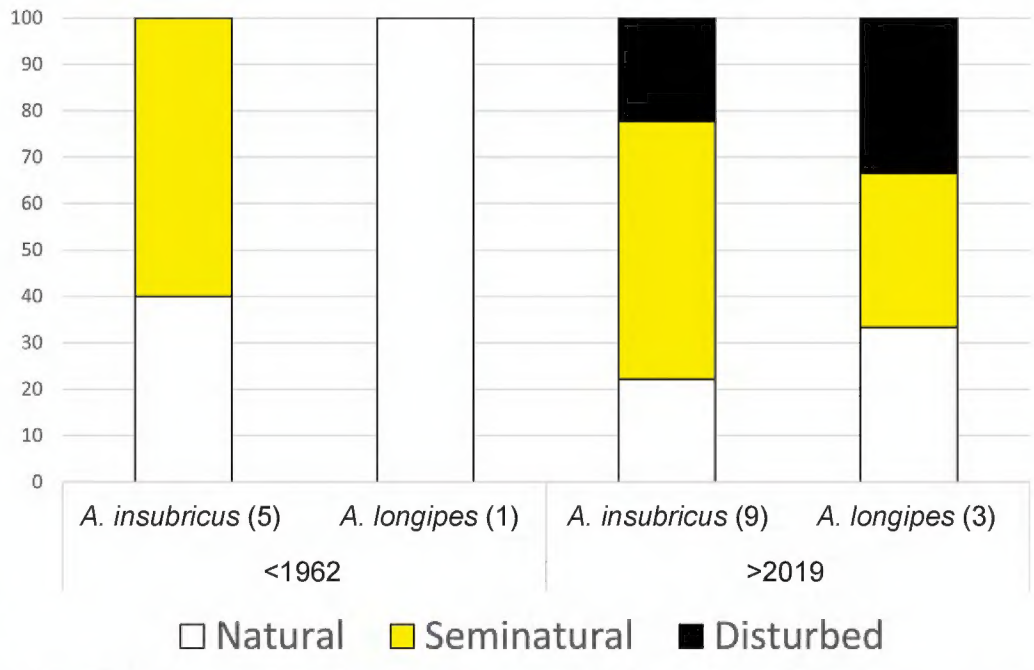

Fig. 4. Habitat disturbance (% sites within three disturbance categories, northern sites in brackets) in the sites of *A. insubricus* and *A. longipes* in two periods along the border of the species' northern range in Slovakia.

Fig. 5. Natural (**A**, Somotor) and disturbed sandy dunes (**B**, Biel) are the typical habitats of both *Acrotylus* species at the border of the species' northern range in southeastern Slovakia (Photo credit: M. Balla).

Conclusions

Both *A. insubricus* and *A. longipes* recolonize historical sites and can spread on anthropogenic bare sandy substrates along the border of their northern range. This study provides evidence that they may reach high abundances at sites with mostly sparse and short psammophilous vegetation occupied by rich orthopteran assemblages, a finding that contributes to informing regional conservation strategies. Our results suggest that *A. insubricus* has a wider distribution than *A. longipes*. We also confirmed the overwintering of adults only in *A. insubricus* at the northern reaches of its distribution range.

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